South African Journal of Botany 2001, 67: 620–628
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SOUTH AFRICAN JOURNAL
OF BOTANY
ISSN 0254-6299

Differences in seed germination of wild and domesticated common bean (*Phaseolus vulgaris* L.) in response to storage

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Received 22 November 2000, accepted in revised form 2 March 2001

This study compared the effect of storage on the germination of wild and domesticated common bean (*Phaseolus vulgaris* L.). Two sizes (large and small) of intact and mechanically scarified seeds of wild common bean from Saltito, Durango and La Malinche, Tlaxcala, Mexico, and the cultivars Bayo Mecentral and Amarillo were stored at 30°C and 75% RH for 0, 30, 60 and 90 days. Germination in the dark at 25°C was evaluated. In general, mechanical scarification at zero days of storage induced a reduction in the time to the start of germination (5 to 83h) and in the time to complete germination (126 to 341h) of wild seeds, but it did not affect the percentage of germination. After 30d of storage the germination of small intact wild seeds from Tlaxcala and cv. Bayo Mecentral was reduced to 30%; but after 60d of storage, wild small seeds from Tlaxcala and both cultivars were almost 100% inhibited. In contrast, as an average, intact and scarified wild seeds from Durango and larger seeds from Tlaxcala reached 52 and 25% of germination respectively. Although 90d of storage affected drastically both wild and domesticated beans, even after this long storage, 3 to 15% of wild seeds germinated. The results are consistent with the speculation that an increased sensitivity of common bean seeds to storage under high temperature and elevated RH could be a concomitant result of selection for some other traits such as large seed during domestication.

Introduction

Domesticated common bean evolved from ancient wild beans that grow in Mesoamerica and other regions of America (Gepts 1991, Smartt 1988). Some aspects recognised as responsible for the genetic diversity among domesticated *Phaseolus* spp. are: the reproductive organs, specifically pods and seeds, which were probably of major interest to humans because of their staple food value, and migration, mutation, human and natural selection and introgression.

Morphological and physico-chemical changes in the seeds of the cultivars of common bean have been identified as a result of domestication. Some of these differences are: an increase in seed size and seed coat colour diversity (Evans 1976), greater susceptibility to insect pests (Smartt 1976, 1988), reduction in cooking time and dormancy (Smartt 1988), and probably a low tolerance to storage under high temperature and humidity (Peña-Valdivia *et al.* 1999a).

Once any cultivar of *P. vulgaris* L. has been harvested, it is a common practice to store the seeds to be used later for food or in sowing for the next crop season. Storage time may differ from a few days to months, even years, before they are used. The physical conditions during the storage time determine whether seed physiological integrity is altered. Relative humidity, which regulates seed moisture content, and the temperature, which affects the rates of biochemical processes in seeds, are the two most important environmental factors that influence the speed of seed ageing. Values higher than 70% RH and 25°C may cause loss of viability and vigour, seed hardening and loss of nutritional value. Some seed traits like genotype, age, size, pre-storage history and moisture content have been recognised as determining to a large extent the response to storage (Delouche and Baskin 1973). Recently it was found that seeds from a wild population of common bean were quite resistant to inadequate storage conditions in which normally domesticated cultivars would be affected (Peña-Valdivia *et al.* 1999a). In that preliminary study, it was observed for a sample of wild seeds that cooking time, percentage germination and vigour of seedlings were not significantly affected after 60 days storage at 30°C and 75% RH (Peña-Valdivia *et al.* 1999a). These authors pointed out that although it was necessary to study more wild samples, it seems that in addition to the morphological, anatomical, physiological and biochemical changes so far identified as a result of domestication, an intrinsic sensitivity to inadequate storage has been selected indirectly and simultaneously with the desired characters in domesticated common bean. To demonstrate this possibility it is necessary to compare the variability between and within wild bean populations and cultivars of common bean, taking into account aspects such as seed coat colour, seed size and geographical origin, under storage conditions involving extremes of temperature and RH. It is also necessary to evaluate wild samples from contrasting geographical origins to detect whether or not the tolerance to these extreme storage conditions is a common trait of wild bean. Since heterogeneity of seed coat impermeability among wild bean samples has been observed (García *et al.* 1999, López *et al.* 1999, Peña-Valdivia *et al.* 1999b) it also seems relevant to examine the role of the seed coat in protecting the wild seed from storage damage. Therefore the objective of this study was to compare the effect of the combination of high temperature and relative humidity during storage on the germination of intact, scarified wild and domesticated seeds of common bean. It is postulated that independently of origin and seed coat impermeability wild common bean has an intrinsic high tolerance to inadequate storage.

Materials and Methods

Biological material

Seeds of common bean (*Phaseolus vulgaris* L.) of two wild populations and two improved cultivars were used in this study (Table 1). The wild seeds were collected from natural populations of common bean from two regions of Mexico. One wild sample is native to Saltito, Durango (WD) and is registered at the Centro Internacional de Agricultura Tropical (CIAT) germplasm bank with the number G11033, DGD-408 (Toro *et al.* 1990); the other wild sample is native to Tlaxcala (WT) (López *et al.* 1999). The cultivars Bayo Mecentral and Amarillo were developed in the INIFAP experimental station at Chapingo, Mexico. The criterion for selecting these materials was the colour of the seed coat, cv. Bayo Mecentral and WD are beige, while cv. Amarillo and WT are yellow, 2.5 Y 8/4 and 2.5 Y 7/10, respectively, according to the Munsell Colour Charts for Plant Tissues (Anonymous undated).

Before beginning the storage experiments seed stocks were reproduced under the same environmental conditions. Seeds were sown during the spring-summer season in 1994, in an experimental plot at Colegio de Postgraduados, Montecillo, Mexico, located at 19° 29' North latitude and 98° 53' West longitude, and 2 250m above sea level, with an average annual temperature of 15.9°C and a mean rainfall of 691mm (García 1988). After harvest, seeds were maintained at 5 ± 1°C until they were used.

The seed size was heterogeneous in both wild bean samples. Therefore, three different sizes were recognised in each seed sample: small, medium and large, which took into account their length, width, thickness and weight. Despite the similar seed size of the improved cultivars, they were also classified by size. These measurements were estimated using a caliper scaled in 1.0mm units and 0.05mm vernier (accuracy to ± 0.01mm), and weighed with an analytical balance (0.0001g). For the purposes of this study and based on the results of the statistic analysis (Table 2), only the small and large seeds were selected for use in the storage study. These two seed sizes were labelled as small wild Durango (SWD), large wild Durango (LWD), small wild Tlaxcala (SWT) and large wild Tlaxcala (LWT). In the case of cultivars, no statistical differences were found, so only one size, equal to seed average weight of each cultivar, was considered. Multiple comparisons for significantly different seed sizes were obtained through the Tukey test (SAS Institute 1988).

Experimental design

A completely random design with factorial arrangement of treatments and four replicates was selected. The controlled variables were: cultivars and wild bean subsamples (cv. Amarillo, cv. Bayo Mecentral, SWD, LWD, SWT and LWT), seed coat (scarified and intact) and storage time (zero, 30, 60 and 90 days). The experimental unit was ten seeds, with no external defects, in a petri dish.

Superficial seed disinfection

Before the storage and germination test the seeds were disinfected superficially for five minutes in a commercial hypochlorite solution (3ml l^{-1} of water). After 5 minutes the seeds were rinsed five times with distilled water and then blotted dry with a paper towel.

Table 1: Population samples, locations of origin, climate and seed characteristics

Population	Location	Climate and annual mean temperature*	Seed† Size (g/100 seeds)	Seed† Colour
Durango (WD)	Saltito, Durango (23°58' Lat N, 104°18' Lon W, 1 820m a.s.l.)	BS1kw(w)(e), and 17.7°C	5.5	Beige 2.5Y8/4
Tlaxcala (WT)	La Malinche, Tlaxcala (19°25' Lat N, 98°8' Lon E, 2 404m a.s.l.)	Cw2(w)(i')g, and 15°C	7.2	Yellow 2.5Y7/10

*According to García (1988); † Munsell Colour Charts for Plant Tissues (Anonymous, undated)

Table 2: Dimensions and weight of wild and domesticated common bean (*Phaseolus vulgaris L.*) seed samples

	Seed size	Length (cm)	Width (cm)	Thickness (cm)	Weight (g)
Saltito, Durango					
	Small	0.595f	0.424e	0.229e	0.039g
	Medium	0.649e	0.462d	0.231e	0.049f
	Large	0.742d	0.520b	0.267d	0.076d
La Malinche, Tlaxcala					
	Small	0.597f	0.455d	0.255d	0.051f
	Medium	0.667e	0.488c	0.262d	0.067e
	Large	0.781c	0.534b	0.313c	0.099c
Cv. Bayo Mecentral					
	Small	0.986b	0.725a	0.527a	0.277a
	Medium	1.087b	0.709a	0.502a	0.298a
	Large	1.127b	0.724a	0.531a	0.281a
Cv. Amarillo					
	Small	1.192b	0.712a	0.450b	0.224b
	Medium	1.200a	0.720a	0.470b	0.282a
	Large	1.252a	0.750a	0.483b	0.297a

N = 50; different letters indicate statistically significant differences for multiple comparisons of seed size for wild samples and cultivars ($P<0.05$)

Scarification

Scarification consisted of making a 1.0mm deep cut in the seed coat with a scalpel, in the region opposite to the micropyle.

Storage conditions

Seeds of each genotype (100g) were placed in loose nylon net bags, above a saturated NaCl solution in 500ml glass jars to generate a 75% RH (Pearcy *et al.* 1991). Under these conditions, seeds were stored for zero, 30, 60 or 90 days at 30 ± 1°C.

Germination

At the end of each storage period seed germination was recorded at 25°C in the dark, in petri dishes with moistened filter paper. Germination was defined as exposition of a 10–20mm long radicle (Ellis *et al.* 1985). Seed germination was recorded every 4h. Percentage of germination and rate of germination was determined for each treatment.

Results

Intact non-stored seeds

Intact wild and domesticated non-stored (time 0) seeds started to germinate (time when at least one seed of each treatment in all repetitions had germinated) about 30h after starting the experiment, but LWD seeds took almost four times longer (116h) than the other seeds to start germination (Table 3). Although most SWD, SWT and LWT seeds germinated within eight days, a small proportion (1–2 seeds) in some replications of these subsamples was highly impermeable, and germination of these seeds occurred between 31 and 38d after the start of incubation. Data for these seeds were excluded from the statistical analysis and from Figure 1.

Among the wild seeds, LWD seeds took significantly more time than the other subsamples to complete germination. After eight days only 40% of the seeds had germinated and, on average, this subsample reached 100% germination after 16d. As was expected, seeds from each cultivar germinated relatively synchronously and although there was a significant difference in the total time to germination between cultivars, the domesticated lines germinated faster (2–2.5d) than the majority of the wild bean subsamples (Table 3; Figure 1).

Despite the differences in the time to the start of germination almost all bean subsamples reached 100% germination (Table 3).

Scarified non-stored seeds

Mechanical scarification reduced significantly the time to the start of germination of LWD and SWT subsamples (83h and 15h, respectively) but the reductions observed in the other two wild subsamples were not significant. In addition, mechanical scarification reduced significantly the time to complete germination of all wild bean subsamples. This reduction ranged between 126h and 341h. In contrast, mechanical scarification affected neither the onset nor completion of germination of seeds of the cultivars (Table 3).

Intact and scarified stored seeds

Thirty days of storage of intact wild seeds from Durango (SWD and LWD) induced a reduction in the time to the start of germination (8h and 95h; $P = 0.040$ and $P = 0.003$, respectively), but intact wild seeds from Tlaxcala (SWT and LWT) were not affected significantly. In addition, the reduction in the time to the onset of germination of wild seeds from Durango, following the combination of scarification and 30d of storage, was not significant. In contrast, storage combined with scarification increased the time to the onset of germination in wild seeds from Tlaxcala by 20h (SWT) and

Table 3: Germination of intact and mechanically scarified seeds of wild and domesticated common bean (*Phaseolus vulgaris* L.) after 30d and 60d of storage at 30°C and 75% RH

Time of storage	Time				Germination	
	to start germination (h)		to complete germination (h)		(%)	
	Intact	Scarified	Intact	Scarified	Intact	Scarified
Zero days						
Small wild from Durango	30bc	25bc	157b	31d	98a	98a
Large wild from Durango	116a	33b	388a	47cd	100a	100a
Small wild from Tlaxcala	31b	16c	179b	25d	100a	100a
Large wild from Tlaxcala	31b	22bc	172b	34cd	97a	97a
cv. Bayo Mecental	35b	28bc	49b	39cd	100a	100a
cv. Amarillo	26bc	23bc	60c	39cd	100a	100a
30 days						
Small wild from Durango	22b	23b	49c	45c	100a	100a
Large wild from Durango	21b	22b	64bc	64bc	100a	100a
Small wild from Tlaxcala	33a	36a	88b	104a	70c	23d
Large wild from Tlaxcala	35a	32a	68bc	66bc	98ab	93b
cv. Bayo Mecental	36a	36a	74bc	75bc	73c	90ab
cv. Amarillo	36a	36a	82b	71bc	95ab	95ab
60 days						
Small wild from Durango	40d	48cd	72b	108a	73a	33b
Large wild from Durango	48bc	72b	108a	80b	35bc	23c
Small wild from Tlaxcala	64	–	64	–	3	0d
Large wild from Tlaxcala	52b	48b	112a	48c	48b	20c
cv. Bayo Mecental	–	73	–	96	0	12
cv. Amarillo	72	86	72	100	2	5
90 days						
Small wild from Durango	116	–	132	–	15	0
Large wild from Durango	–	–	–	–	0	0
Small wild from Tlaxcala	64	–	64	–	3	0
Large wild from Tlaxcala	–	–	–	–	0	0
cv. Bayo Mecental	–	–	–	–	0	0
cv. Amarillo	–	–	–	–	0	0

Different letters indicate statistically significant differences for multiple comparisons within time of storage treatments ($P<0.05$). Some data were not included in the statistical analysis because there were no sufficient repetitions

10h (LWT) ($P = 0.0006$ and $P = 0.0304$). Thirty days of storage of intact and scarified cultivar seeds did not modify significantly the time to the onset of germination.

Significant reductions (between 324 and 91h; $P \leq 0.0001$) and synchronisation of the time to complete germination of both small and large intact wild seeds from Durango and Tlaxcala were induced with 30d of storage. In contrast, storage of scarified wild seeds for 30d slightly increased the time to complete germination (Table 3). Under the same conditions, the time to complete germination was increased by an average of 31h in intact and scarified seeds of the cultivars, Bayo Mecentral and Amarillo (Table 3).

In both intact and scarified seeds the capacity to germinate was reduced by different proportions after 30 days of storage. In particular, SWD, LWD and LWT seeds were not affected. However, the capacity of intact and scarified SWT seeds to germinate was reduced by 30% and 77%, respectively. Amongst the cultivars studied only scarified Bayo Mecentral seeds were affected by 30d storage with germination reduced 27% (Table 3, Figure 2).

Increasing the storage time of wild seeds to 60d increased the time to the onset of germination in both intact and scarified seeds by between 10 and 39h. The exception was intact LWD seeds in which 60d storage, like 30d storage, reduced the time to the start of germination. In this case the reduction was 68h (Table 3).

Sixty days of storage reduced the percentage germination of intact seeds to a different degree from that of non-stored seeds. Among wild seeds, SWT seeds were the most affected and germination of both cultivars was almost totally inhibited. In these cases, the data of time to start and to complete germination was the same because in some repetitions only one seed germinated. For this reason these data were not included in the statistical analysis (Table 3, Figure 3). In contrast, germination of both subsamples from Durango (SWD and LWD) and the atypical, or large-seed subsample from Tlaxcala (LWT) was only affected by 27, 65 and 52%, respectively (Table 3, Figure 3).

Combination of scarification and 60d of inadequate storage inhibited SWT germination completely (Figure 3), whereas germination of SWD, LWD and LWT was only inhibited by 67, 77 and 80%, respectively (Table 3, Figure 3). Germination of both cultivars was also reduced under these conditions of storage by 88 and 95%, respectively (Table 3, Figure 3). Likewise, 60 days of exposure to this storage condition, completely inhibited the cv. Bayo Mecentral germination and almost totally inhibited the cv. Amarillo and SWT, while in SWD, LWD and LWT germination was reduced only partially

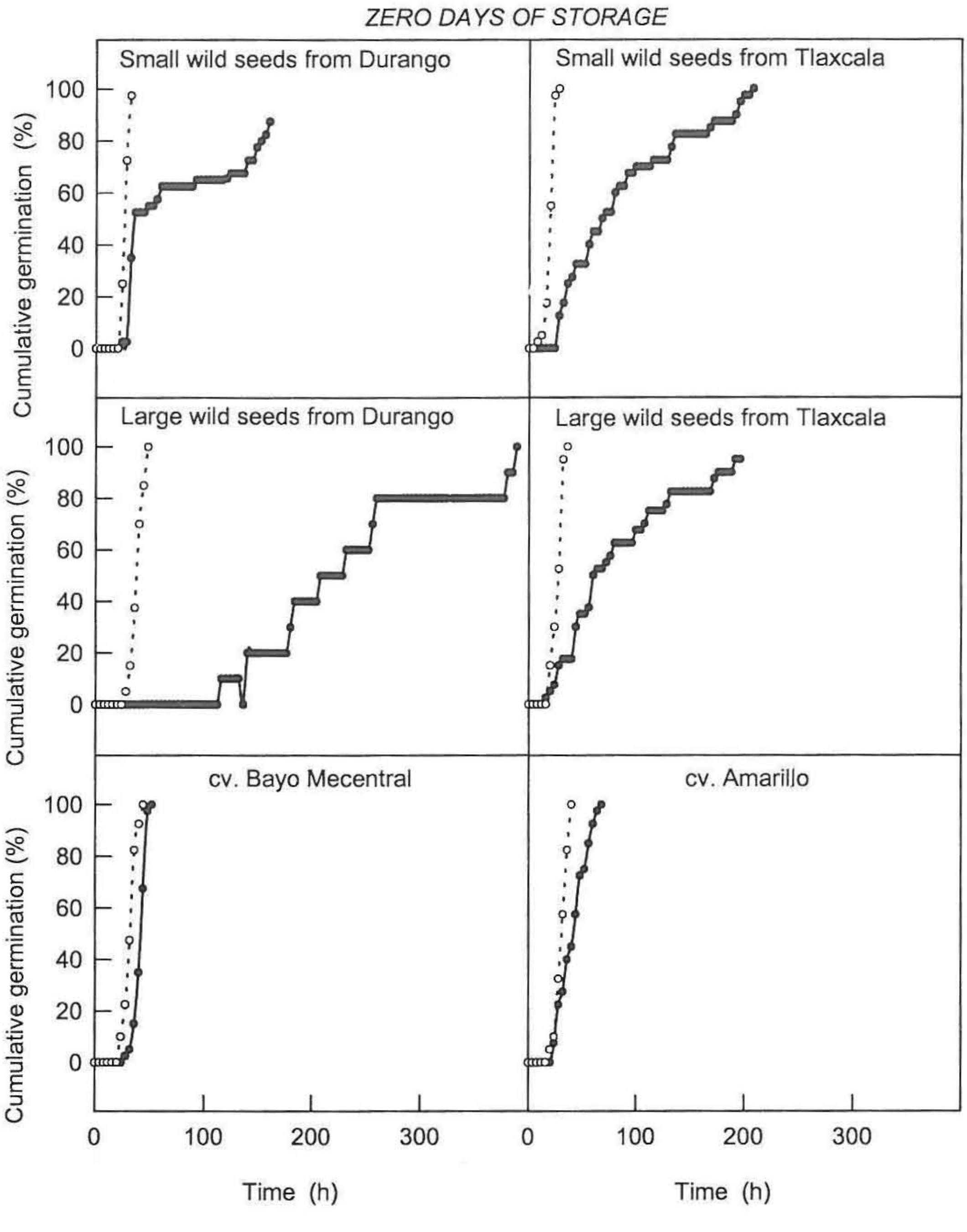

Figure 1: Germination curves of wild common bean (*Phaseolus vulgaris* L.) from Durango and Tlaxcala, and the cultivars Bayo Mecentral and Amarillo. Intact (solid circles) and mechanically scarified seeds (open circles) after zero days of storage at 30°C and 75% RH

(by 27, 65 and 50%, respectively) (Table 3, Figure 3).

When the storage time was increased to 90d both wild and domesticated seeds were affected drastically but even with this long storage time, intact SWD and SWT reached 15% and 3% germination, respectively (Table 3).

Discussion

Physiological and biochemical alterations in seeds of domesticated common bean following exposure to inadequate storage conditions, *i.e.* either low or high temperatures, have been documented widely (Begnami and Cortelazzo 1996, García 1994, Hentges *et al.* 1991, Hincks and Stanley 1986, Jackson and Varriano-Marston 1981, Moscoso *et al.* 1984, Pandey 1989, Peña-Valdivia *et al.* 1999a, Srisuma *et al.* 1989). Such alterations are the result of changes in the structure and activity of proteins, polysaccharides, lipids, nucleic acids, and loss of membrane integrity, which can lead to a reduction or a total loss of viability, a reduction in the nutritional value, an increase in the cooking time, and changes in

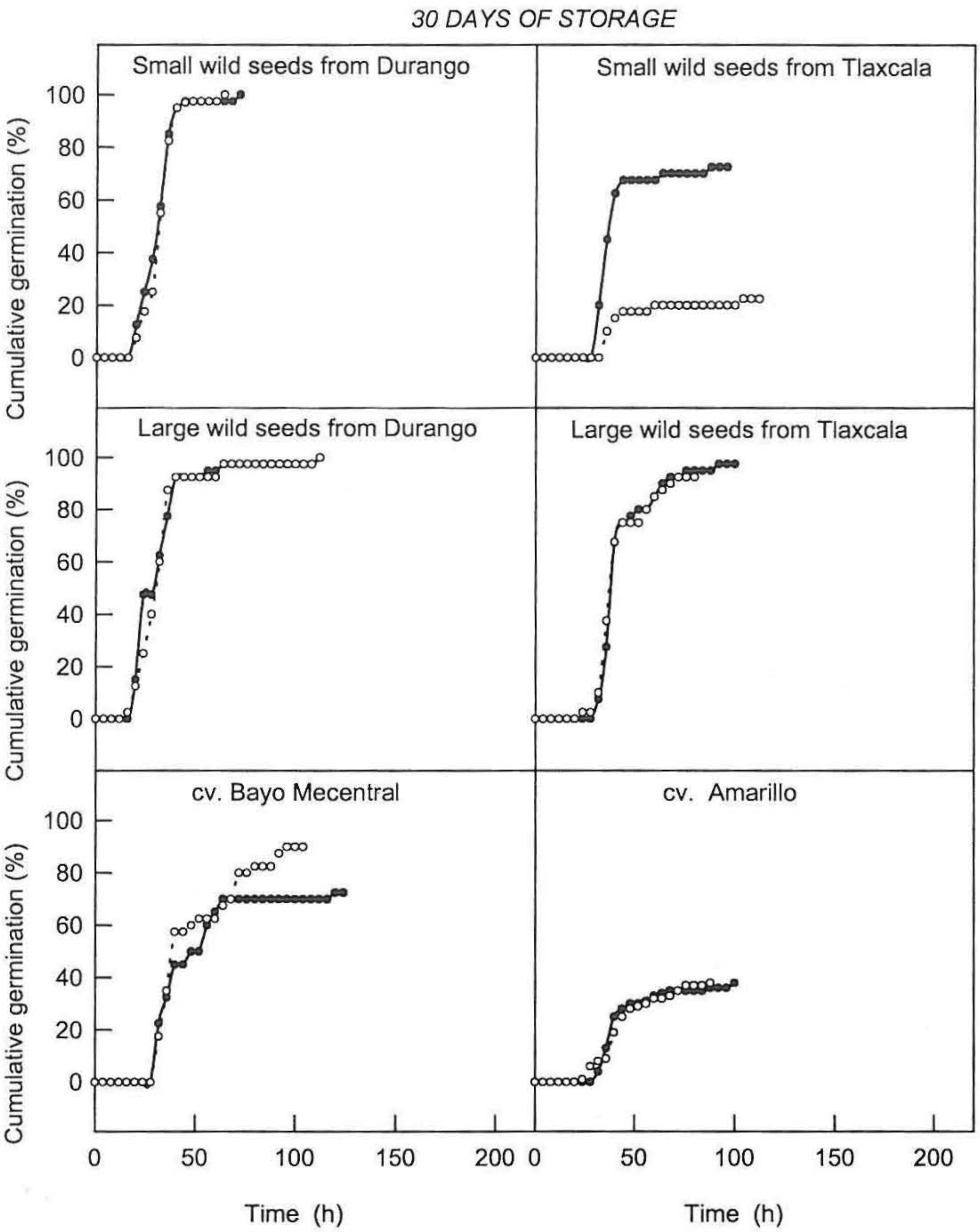

Figure 2: Germination curves of wild common bean (*Phaseolus vulgaris* L.) from Durango and Tlaxcala, and the cultivars Bayo Mecentral and Amarillo. Intact (solid circles) and mechanically scarified seeds (open circles) after 30d of storage at 30°C and 75% RH

the coat colour. All these alterations and their magnitude are apparently genetically determined. The variability observed among the individuals of a seed population has led to the recognition of at least three categories: 1) those seeds that never reach a capacity to germinate, 2) those that reach a capacity to germinate and maintain this capacity even in the face of environmental changes, and 3) those that reach a capacity to germinate, but in which that capacity is partially or completely lost due to their high susceptibility to some environmental conditions (Roberts 1972).

The improved cultivars used in this study (Bayo Mecentral and Amarillo) seem to belong to the third category mentioned above. According to Begnami and Cortelazzo (1996), Bressani (1993), Hentges *et al.* (1991), Hincks and Stanley (1986), Jackson and Varriano-Marston (1981), Moscoso *et al.* (1984), Pandey (1989), Peña-Valdivia *et al.* (1999a), and Srisuma *et al.* (1989) seeds of nearly all bean cultivars that are now utilised as staple food have their maximum germination capacity at harvest, but they are very sensitive to storage under temperature higher than 20°C and RH between

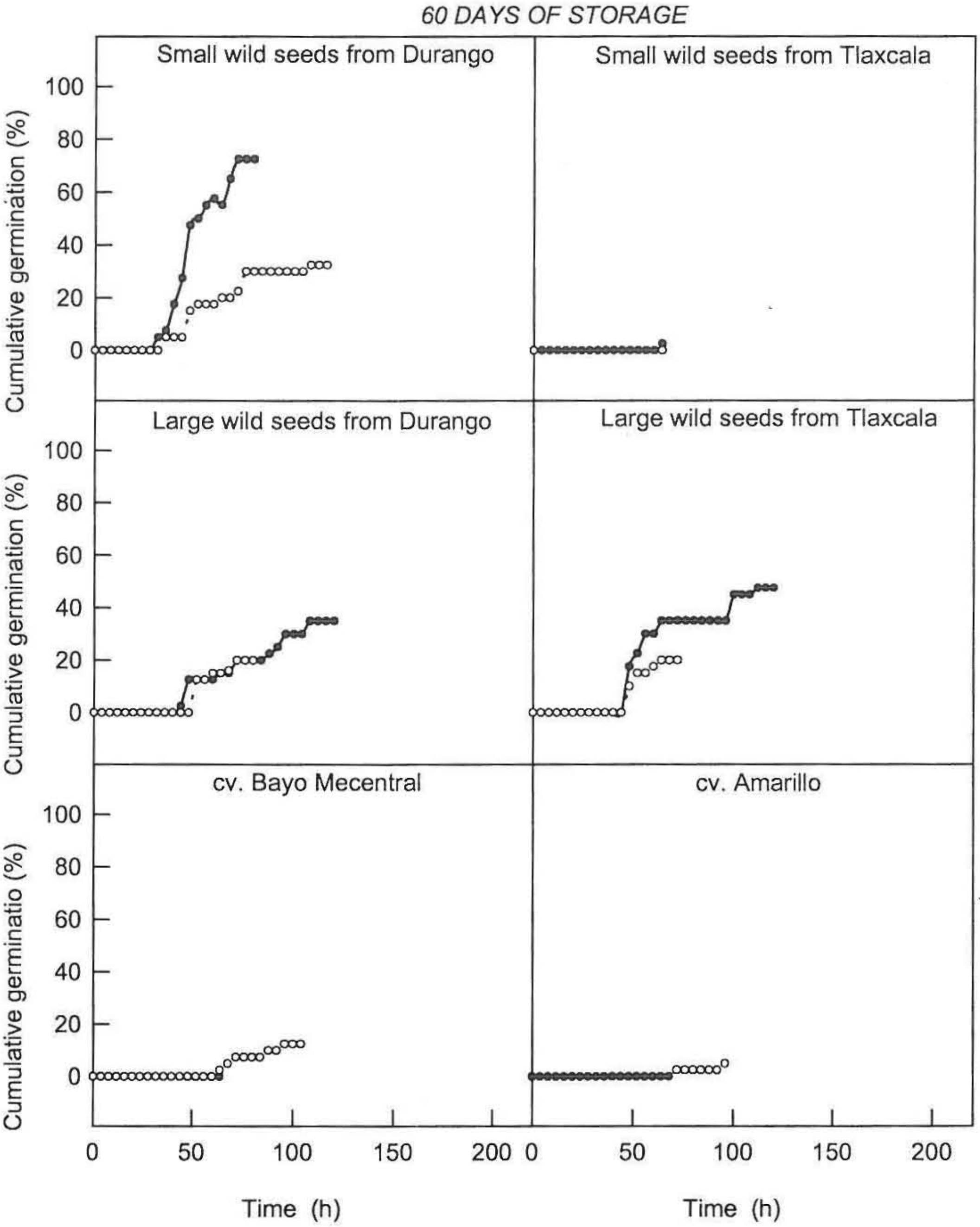

Figure 3: Germination curves of wild common bean (*Phaseolus vulgaris* L.) from Durango and Tlaxcala, and the cultivars Bayo Mecentral and Amarillo. Intact (solid circles) and mechanically scarified seeds (open circles) after 60d of storage at 30°C and 75% RH

75 and 100%. These seeds lose their capacity to germinate in short periods of time under such conditions. Hard seed characteristics, which are apparently related to coat structure and confer some degree of resistance to ageing, have also been observed in some cultivars of common bean (Dickson 1980). Seed coats of the wild seeds included in the present work were not totally responsible for protection from the storage environment, because 30d of storage did not affect the time to start and to complete germination and the percentage of germination in both intact and scarified SWD, LWD, and LWT seeds (Table 3, Figure 2). Besides, 60d of storage of scarified wild seeds accelerated the germination of LWD and LWT and diminished significantly the percentage germination only in SWD and LWT (Table 3, Figure 3).

The results of this study clearly demonstrate a different tolerance to inadequate storage conditions between wild bean seeds and the improved cultivars. Initially, it was thought that wild common bean would be more resistant to inadequate storage conditions. This speculation was partially correct, because it was also found that there were significant differences between the two wild common bean used in this work in their sensitivity to inadequate storage conditions. SWD and SWT achieved 15% and 3% respectively of germination even at 90 days of inadequate storage. In contrast, in the other seeds germination was completely inhibited after this storage period. It was observed that wild seeds from Durango had the highest tolerance to storage. We do not known why these two wild seed samples had apparently different sensitivities to inadequate storage conditions, but the reasons may be related to their quite different origins where the environmental conditions play an important role in determining their respective resistance to the local adverse conditions. Wild seed from Durango grow spontaneously at 1 820 metres above sea level in a semiarid climate where the temperature can be extreme, with a short rainy period in summer. In contrast, wild seeds from Tlaxcala grow at 2 404 metres above sea level, in a region with higher rainfall and relative humidity and lower temperature (García 1988).

The results of the present study demonstrate clearly an inverse relationship between tolerance to inadequate storage and seed size of common bean subsamples from Durango. These subsamples, as well as the cv. Bayo Mecentral, the less tolerant to inadequate storage present beige seed coat, and are consistent with the hypothesis that an increased sensitivity of common bean seed to high temperature and high RH storage could be an indirect result of selection during domestication of some other traits such as bigger seed size (Peña-Valdivia *et al.* 1999a). This relation has already been suggested for other domesticated plant species (Heiser 1988).

It is a fact that wild bean seeds are exposed naturally to significant fluctuations in temperature and RH (Bewley and Black 1994, Mayer and Poljakoff-Mayber 1989), and it is very likely that they have intrinsic characteristics which confer more tolerance to them under extreme environmental conditions, such as those present under inadequate storage conditions. Intact non-stored seeds of the cultivars Bayo Mecentral and Amarillo had a mean germination time of 50h; in contrast all wild seeds under the same conditions had a slow rate of germination, needing on average 222h to germinate. However, scarification increased the rate of germination to an average time of 39h in the cultivars and 35h in the wild seeds (Table 3 and Figure 1).

After thirty days of storage a reduction in the germination time of intact wild seeds was observed; the reduction (between 100–260h) was similar to that observed in the scarified seeds (Figures 1 and 2). On average, both intact and scarified wild seeds stored for 30d require 100h to reach maximum germination (Figure 2). It can be also observed that after inadequate storage, cultivars needed more time to germinate in comparison with the control. A treatment of 60d under the inadequate storage conditions did not increase the germination time and scarification had no additional effect on the germination rate (Figure 3). The germination time for SWD and SWT after 90d of storage was 152h and 104h, respectively.

Conclusions

The results of this study demonstrate clearly that wild seeds are dormant. This dormancy was broken when they were scarified or stored at high temperatures and elevated R.H. Wild seeds had a great tolerance to inadequate storage conditions, which contrasted with the high sensitivity of the two cultivars. Differences in tolerance to inadequate storage conditions between the two wild seed samples were apparent. Smaller seeds with a beige coloured seed coat were more tolerant to sub-optimal storage conditions. It is difficult to explain such differences but they may be related to the peculiarities of the environmental conditions in the region from which each sample was collected.

Acknowledgements — The authors wish to thank Dr William A Cress for critically reading of the manuscript.

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Edited by TH Thomas